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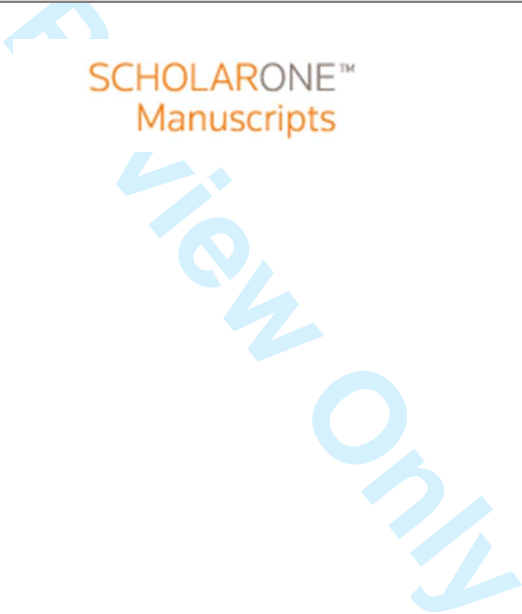
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Abstract:	<p>1. Impacts of bottom fishing, particularly trawling and dredging, on seabed (benthic) habitats are commonly perceived to pose serious environmental risks. Quantitative ecological risk assessment can be used to evaluate actual risks and to help guide the choice of management measures needed to meet sustainability objectives.</p> <p>2. We develop and apply a quantitative method for assessing the risks to benthic habitats by towed bottom-fishing gears. The method is based on a simple equation for relative benthic status (RBS), derived by solving the logistic population growth equation for the equilibrium state. Estimating RBS requires only maps of fishing intensity and habitat type — and parameters for impact and recovery rates, which may be taken from meta-analyses of multiple experimental studies of towed-gear impacts. The aggregate status of habitats in an assessed region is indicated by the distribution of RBS values for the region. The application of RBS is illustrated for a tropical shrimp-trawl fishery.</p>

	<p>3. The status of trawled habitats and their RBS value depend on impact rate (depletion per trawl), recovery rate and exposure to trawling. In the shrimp-trawl fishery region, gravel habitat was most sensitive, and though less exposed than sand or muddy-sand, was most affected overall (regional RBS=91% relative to un-trawled RBS=100%). Muddy-sand was less sensitive, and though relatively most exposed, was less affected overall (RBS=95%). Sand was most heavily trawled but least sensitive and least affected overall (RBS=98%). Region-wide, >94% of habitat area had >80% RBS because most trawling and impacts were confined to small areas. RBS was also applied to the region's benthic invertebrate communities with similar results.</p> <p>4. Conclusions. Unlike qualitative or categorical trait-based risk assessments, the RBS method provides a quantitative estimate of status relative to an unimpacted baseline, with minimal requirements for input data. It could be applied to bottom-contact fisheries worldwide, including situations where detailed data on characteristics of seabed habitats, or the abundance of seabed fauna are not available. The approach supports assessment against sustainability criteria and evaluation of alternative management strategies (e.g. closed areas, effort management, gear modifications).</p>



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6 **Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a**
7 **simple quantitative risk assessment method applicable to data-limited fisheries.**

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25 **Summary**

26 **1.** Impacts of bottom fishing, particularly trawling and dredging, on seabed (*benthic*) habitats are commonly
27 perceived to pose serious environmental risks. Quantitative ecological risk assessment can be used to evaluate
28 actual risks and to help guide the choice of management measures needed to meet sustainability objectives.

29 **2.** We develop and apply a quantitative method for assessing the risks to benthic habitats by towed bottom-
30 fishing gears. The method is based on a simple equation for relative benthic status (RBS), derived by solving
31 the logistic population growth equation for the equilibrium state. Estimating RBS requires only maps of fishing
32 intensity and habitat type — and parameters for impact and recovery rates, which may be taken from meta-
33 analyses of multiple experimental studies of towed-gear impacts. The aggregate status of habitats in an
34 assessed region is indicated by the distribution of RBS values for the region. The application of RBS is
35 illustrated for a tropical shrimp-trawl fishery.

36 **3.** The status of trawled habitats and their RBS value depend on impact rate (depletion per trawl), recovery
37 rate and exposure to trawling. In the shrimp-trawl fishery region, gravel habitat was most sensitive, and
38 though less exposed than sand or muddy-sand, was most affected overall (regional RBS=91% relative to un-
39 trawled RBS=100%). Muddy-sand was less sensitive, and though relatively most exposed, was less affected
40 overall (RBS=95%). Sand was most heavily trawled but least sensitive and least affected overall (RBS=98%).
41 Region-wide, >94% of habitat area had >80% RBS because most trawling and impacts were confined to small
42 areas. RBS was also applied to the region's benthic invertebrate communities with similar results.

43 **4. Conclusions.** Unlike qualitative or categorical trait-based risk assessments, the RBS method provides a
44 quantitative estimate of status relative to an unimpacted baseline, with minimal requirements for input data.
45 It could be applied to bottom-contact fisheries worldwide, including situations where detailed data on
46 characteristics of seabed habitats, or the abundance of seabed fauna are not available. The approach supports
47 assessment against sustainability criteria and evaluation of alternative management strategies (e.g. closed
48 areas, effort management, gear modifications).

49 **Key-words:** ecosystem-based fishery management; ecological risk assessment; effects of trawling; trawl
50 footprints; benthic fauna; vulnerability indicators; depletion; recovery; resilience; sensitivity

51 Introduction

52 Globally, bottom trawling and dredging interact directly with larger areas of seabed habitat than other human
53 activities (Kaiser et al. 2002) and are widely perceived to have significant direct and indirect impacts on these
54 habitats (Jennings & Kaiser 1998). Recognition of the collateral consequences of fishing, including habitat
55 impacts by trawling, has led to the broader ecosystem being considered in managing fisheries (“ecosystem-
56 based fishery management”; Pikitch et al. 2004) and to the emergence of policy commitments and
57 requirements from sustainable-seafood certification bodies to take account of ecosystem impacts of fishing in
58 management plans (e.g. Rice 2014). Increasingly, this is occurring as part of national and international
59 adoption and implementation of an “Ecosystem Approach to Fisheries” (FAO 2003; Sinclair & Valdimarsson
60 2003). These policies demand levels of evidence that often do not exist, or are too costly to obtain, at scales of
61 management regions. When resources are limited, a common approach for supporting management is risk
62 assessment, which seeks to describe the magnitude of fisheries impacts and requirements for measures to
63 meet management objectives. However, methods for risk assessment vary in their complexity and capacity to
64 support management (Smith et al. 2007).

65 Initially, environmental risk assessments for the effects of fishing (ERAEF) were based on a ‘likelihood–
66 consequence’ approach (e.g. Fletcher et al. 2002) and/or a qualitative ‘susceptibility–resilience’ approach (e.g.
67 Stobutzki, Miller & Brewer 2001) and often, expert judgment was used for scoring (e.g. Eno et al. 2013). These
68 non-quantitative, typically non-spatial, approaches provide estimates of relative levels of susceptibility or
69 potential risk, but have limited ability to assess sustainability. More recently, quantitative (Zhou & Griffiths
70 2008) and quantitative-spatial (Pitcher 2014) ERAEF approaches have been developed and applied. These
71 provide estimates of absolute status and thus support more refined advice about management measures
72 needed to meet sustainability objectives. These different levels of ERAEF were placed in a 3-tier ‘triage’
73 framework by Hobday et al. (2011) where risk is assessed by more detailed level 2 or 3 methods (with greater
74 data demand and cost expected) if less detailed level 1 or 2 methods indicate that risk is non-negligible.

75 In trawl fisheries, ERAEF has largely focused on non-target or bycatch species at level-2 (e.g. Stobutzki Miller &
76 Brewer 2001; Astles et al. 2006), with recent level-3 assessments providing quantitative estimates of bycatch

sustainability (e.g. Zhou & Griffiths 2008; Pitcher 2014). However, habitat ERAEF (e.g. Williams et al. 2011) are less commonly implemented and typically less developed, with only a few examples of level-3 quantitative spatial assessments (e.g. Pitcher et al. 2015a,b). The slower development of habitat ERAEF may be due to the paucity of suitable data for habitats and the perception that habitats are intractable to model in a generalized way, because they comprise or harbour many interacting species with complex dynamics. However, some studies indicate that aggregate properties of seabed habitats and communities do respond in predictable ways to trawling impacts (Collie et al. 2000; Kaiser et al. 2006); thus their collective dynamics can be parameterised and used in quantitative assessment models (e.g. Ellis, Pantus & Pitcher 2014). The reduced variation in aggregate parameters may be important from an ecological perspective, because some species in a community will be more sensitive to impacts, have slower recovery times or interact more strongly with other species. Nevertheless, assessment of trawl risk at the level of habitat has clear management relevance considering that management objectives and certification requirements often focus on habitats rather than species (MSC 2014; Rice, Lee & Tandstad 2015). Attribution of parameters to overall dynamics enables quantitative status assessment for habitats and communities. Such assessments require information on their sensitivity to impacts, recovery rates, distributions, and exposure to trawling,. Here, we develop a simple, widely applicable quantitative level-3 ERAEF method for assessing relative benthic status (RBS) in areas fished with towed bottom-contact gears. As an example application, we assess RBS for seabed habitats and benthic invertebrate taxa in a tropical trawl fishery.

Methods

DEVELOPMENT OF THE RBS METHOD

The dynamics of the abundance of seabed communities are assumed to be described by a Schaefer (1954)-type logistic population growth equation, with an additional term to describe the direct impacts of trawling on the seabed, consistent with previous ERAEF approaches (e.g. Smith et al. 2007; Ellis, Pantus & Pitcher 2014),

$$\delta B/\delta t=RB(1-B/K)-DFB$$

eqn 1

where $\delta B/\delta t$ is the rate of change in abundance B in time t , R is recovery rate, K is carrying capacity, D is trawl depletion rate (specific to different gear-types) and F is trawling effort as swept-area ratio (the total area swept by trawl gear within a given area of seabed, divided by that seabed area). This model has been used for dynamic assessments of benthos faunal status (e.g. Ellis, Pantus & Pitcher 2014) and to evaluate the effects of management (e.g. Pitcher et al. 2015a,b). Typically, assessment regions are gridded and the model (eqn 1) applied within every cell, assuming that the fauna in each grid cell respond independently to trawling. This assumption is considered acceptable for relatively immobile benthos, but cell-connectivity parameters could be added for mobile fauna (if available). At the scale of grid-cell sizes typically used (e.g. 0.01° , 1×1 nmi, 3×3 km, 0.1° — Pitcher et al. 2015a; Dichmont et al. 2013; Hiddink et al. 2006a; Ellis, Pantus & Pitcher 2014), other studies have observed differences in benthos abundances related to patterns of trawling intensity defined on similar scales (e.g. McConnaughey et al. 2000; Piet et al. 2000; Pitcher et al. 2000; Lambert et al. 2011).

The usual implementation of the logistic equation is dynamic, with trawling-induced mortality input as a time-series and abundance output as a time-series. However, for data-limited situations, an approach that does not rely on a time series of inputs is desirable. If the question about risk is framed as “will the current level of fishing lead (or has it led) to habitat status that compromises a defined management objective?”, then a simpler approach can be used to assess status. This involves solving the logistic equation for the equilibrium state (i.e. $\delta B/\delta t=0$), in which case eqn 1 has the solution:

$$B/K = 1 - FD/R \text{ if } F < R/D, \text{ otherwise } B/K = 0 \quad \text{eqn 2}$$

where B/K represents relative benthic status (RBS). Thus the equation can be used when K is unknown, or cannot be clearly defined. The method assumes that the current (or future) level of trawl effort F has been (or will be) applied indefinitely. An analogous approach, based on this assumption, was used to project long-term biomass of benthic species under constant F (Appendix C in Ellis, Pantus & Pitcher 2014).

Estimation of RBS (eqn 2) requires relatively few parameters: habitat type, trawl effort, depletion rates and recovery rates. Regional application of RBS requires maps of habitats and trawl effort; both should be determined for grid cells at a scale that adequately captures within-region heterogeneity of habitats and trawl effort. Grid cells of areas $\sim 1\text{--}5 \text{ km}^2$ typically are small enough that the distribution of fishing effort within those

cells is random (e.g. Rijnsdorp et al. 1998; Deng et al. 2005; Ellis, Pantus & Pitcher 2014). Maps of trawling intensity may be derived from fishing vessel logbooks and/or vessel monitoring systems (VMS); typically as hours of effort. These data need to be gridded at a suitable cell resolution, and converted to trawl swept-area ratio (using information on gear swept-width, tow speeds, and grid-cell area).

Trawl impacts differ among gear types and habitats, and recovery rates differ among habitats. Typically, habitats in stable environments are dominated by longer-lived and more sensitive biota that recover slowly, while habitats exposed to high levels of natural disturbance (e.g. mobile sediments) tend to be dominated by less susceptible biota that recover quickly (Jennings & Kaiser 1998). Parameters for depletion and recovery rates, if not available for habitats in an assessment region, may be obtained from suitable representative meta-analyses of multiple trawl-impact experiments (e.g. Collie et al. 2000; Kaiser et al. 2006). However, experimental-scale depletion and recovery rate estimates (d , r) must be adjusted to grid scale parameters (D , R in eqn 2). If the grid scale is chosen so that trawling is distributed randomly within each cell then $D=d$, but $R=r$ only when trawling is uniform. When trawling is random, the following adjustment is required:

$$R=rd/[-\ln(1-d)] \qquad \text{eqn 3}$$

where d is proportional depletion rate per trawl pass (Ellis, Pantus & Pitcher 2014). In implementation, RBS is estimated for each grid-cell based on trawl effort and appropriate depletion and recovery rates for the gear and habitat. The average RBS and distribution of RBS values over grid cells, by habitat, indicate the landscape scale status of habitats.

APPLICATION OF THE RBS METHOD

We applied RBS to assess the status of habitats in Exmouth Gulf, Western Australia, which is fished for shrimps by otter-trawlers. The region has also been disturbed by cyclones (Loneragan et al. 2013) and extreme heatwaves (Caputi et al. 2016). Gear- and habitat-specific parameters for d and r were extracted from a published meta-analysis (Collie et al. 2000) and linked to maps of habitats and trawling effort in the Gulf. The sediment-habitat categories used in the meta-analysis were also adopted for Exmouth Gulf.

Depletion and recovery rates

Impact effects (i), as log(response ratio), were taken from figure 2 of Collie et al. (2000) for gear type, habitat type, and benthos taxa. Estimates of i for gear-by-habitat and for taxa-by-habitat (for otter trawl) were inferred assuming additivity on the log scale and ignoring the possibility of interactions (Table 1). Impact values were assumed, conservatively, to represent the effect of a single trawl pass, although this may not have been the case in all studies included in the meta-analysis. The impact values (Table 1) for otter trawling in sedimentary habitats, and for three taxa (for which recovery rates could be estimated), were converted to proportional depletion rates d per trawl pass:

$$d=1-e^i \quad \text{eqn 4}$$

Recovery was estimated from figure 5 in Collie et al. (2000), where LOESS curves were presented for 4 habitat types and 3 taxa, based on fits to recovery data. Time taken to recover to reference state differed across habitats (for all taxa pooled), with ~100 days on Sand, ~200 days on Mud and ~300 days on muddy-Sand. Recovery of Gravel was not presented in Collie et al. (2000), but was assumed to be similar to their 'Biogenic' category, at about 500 days given other evidence suggesting that gravel habitats recover more slowly than other sedimentary habitats (e.g. Kaiser et al. 2006). Recovery times also differed among the three taxa presented (for all habitats pooled), with about 200 days for Malacostraca (crustaceans), ~250 for Polychaeta (worms) and ~450 for Bivalvia (2-shelled molluscs).

To estimate r , we solved the logistic equation for B_t (eqn 5; Figure 1) and fitted this model to the LOESS curves in figure 5 of Collie et al. (2000), after first back-transforming the response and re-scaling time from days to years:

$$B_t=B_0K/[B_0+(K-B_0)e^{-rt}] \quad \text{eqn 5}$$

where B_0 is the abundance immediately after experimental impact. B_0 is a function of depletion rate d per trawl and the number of experimental trawls T ; thus, $B_0=K(1-d)^T$ and the complete model is:

$$B_t=K(1-d)^T/[(1-d)^T+(1-(1-d)^T)e^{-rt}] \quad \text{eqn 6}$$

This model was fitted using iterative non-linear regression. K was set to unity since Collie et al. (2000) presented their figure 5 on a log(response ratio) scale (i.e. relative to 1). T was assumed to be unity because, in this instance, d was separately estimated by eqn 4 and to estimate r it was only necessary for the model to fit abundance immediately after impact. If, in future, eqn 6 was used to simultaneously estimate both r and d , the actual value of T would be important.

The recovery information in Collie et al. (2000) was for habitat and taxa main effects only. Habitat-by-taxa recovery rates for 3 taxa in 4 habitats were inferred in the same manner as those for impact effects. The experimental scale r estimates were adjusted, using eqn 3, to grid-scale R .

Regional habitats and trawl effort

Linking these estimates of depletion and recovery to the habitats of Exmouth Gulf requires that the region's habitats are mapped according to the categories used in the meta-analysis. Mapped sediment data for the Gulf were obtained from a global database (dbSeabed, <http://instaar.colorado.edu/~jenkinsc/dbseabed/>, Jenkins 1997) as continuous fractions of mud, sand and gravel. These data are derived from any available direct sediment sampling or observations (e.g. quantitative and textual descriptions of grab/core samples) and subsequently interpolated using an Inverse Distance Weighted method. For the study area ~630 source samples were available, with their average separation of ~2–3 km comparable with the scale of the study grid. The continuous sediment fractions were classified to habitat types matching those of Collie et al. (2000), using a simplified Folk (1954) sediment ternary distribution (Gravel if %gravel>30%, else Sand if %mud<20%, else Mud if %sand<20%, else=muddySand — Figure 2 inset), and mapped.

The distribution and intensity of trawl effort was mapped by interpolating and gridding position data of trawling events recorded in confidential fishing vessel logbooks for a 5-year period (2008–2012). Each trawl event included the associated hours of trawling effort. Gridding was done for 0.01° cells (~1.15 km²), because trawling typically is distributed randomly at this scale (see previous section) and hence $D=d$ in eqn 2. If trawling at this scale was more uniform than random, then depletion would be greater; whereas if it was more aggregated than random, then depletion would be less (Ellis, Pantus & Pitcher 2014). Effort in hours per grid-cell was re-scaled to total swept area, based on gear swept-width (≤ 30 m sweep, for shrimp trawls comprising

4 nets of 5.5 or 6 fathom head-rope length without sweeps or bridles; Kangas et al. 2007) and tow speeds (~3.5±0.3 knots). Total swept area per grid-cell was divided by grid-cell area to provide the swept-area ratio F . Effort distributions were consistent among years, so the assumption of constant F was considered reasonable and the average annual effort was mapped and used in the assessment. The total trawl-footprint area, accounting for overlapping trawling, was estimated using both uniform and random assumptions for effort distribution within cells.

Status assessment

The status of sedimentary habitats in Exmouth Gulf was assessed by setting the un-trawled status of each grid cell to unity and using eqn 2 to estimate RBS for each cell (expressed as a proportion of un-trawled status) from the D , R and F values. By inference, the RBS of habitats represents an average over the mix of benthic taxa typically present in these sediment categories across the range of studies included in the meta-analysis. The Gulf-wide status of habitats, accounting for their different sensitivity and exposure to trawling, was quantified by plotting the distribution of RBS values against proportion of habitat area, by mapping their spatial distribution and by the region-wide average RBS value. RBS was also assessed for three benthos taxa. In addition, their absolute status was estimated using information on their distributions (see Appendix S1).

Results

DEPLETION AND RECOVERY RATES

The status of trawled habitats, and hence their RBS score, depends on their depletion rate, recovery rate and exposure to trawling. Gravel and Malacostraca have the highest depletion rates in response to otter trawling, whereas Mud and Bivalvia have the lowest (Table 2). Sand and Polychaeta have the highest grid recovery rates (R), whereas Gravel and Bivalvia have the lowest (Table 3). The sensitivity of habitats or taxa to trawling is given by the ratio D/R and the critical level of F that would drive their equilibrium status to 0 is R/D . Hence, Gravel is the most sensitive habitat and has critical $F=4.6$, whereas Sand is least sensitive. Malacostraca are the most sensitive taxa and have critical $F=5.7$ (pooled across habitats), whereas Bivalvia are least sensitive.

220 REGIONAL HABITATS AND TRAWL EFFORT

221 Most (51%) sediments of the ~3,500 km² Exmouth Gulf, between 1–50 m depth, were classified as Sand
222 followed by Gravel (27%, located mainly in the outer Gulf) and muddy-Sand (20%, mainly in the inner Gulf)
223 (Figure 2). There are a few small areas of Mud (2%) close to the coast.

224 Most trawling in the Gulf occurred in depths between 5–25 m and was aggregated in hotspots (Figure 3). No
225 trawling was recorded in half of the total grid cells (Table 4, Figure 4) including areas both closed to trawling
226 and open but not trawled. About 33% of cells were fractionally trawled (leaving ~75% area untrawled in total)
227 and ~17% were trawled more than once per year. The highest swept-area ratio at the 0.01° cell-scale was ~7.8
228 times per year. The trawl footprint calculated assuming random trawling (Table 4) estimates the area trawled
229 in a single year at ~740 km² (~21% of the Gulf). However, because within-cell trawling generally is not fixed in
230 space, the long-run expectation is that the area within each grid cell is trawled at the average swept-ratio
231 (Ellis, Pantus & Pitcher 2014); hence, the uniform assumption is most representative of the multi-year trawl
232 footprint (~892 km² or ~25% of the Gulf).

233 Most trawling footprint, by area, occurred on Sand, followed by muddy-Sand, Gravel and Mud (Table 4).
234 However, relatively, muddy-Sand was proportionally more exposed to trawling followed by Sand and Gravel
235 (Figure 4); there are few areas of Mud and these were least exposed. A similar proportion (~10%) of each
236 habitat, except Mud, was exposed to high effort (swept-ratio >~2).

237 STATUS ASSESSMENT

238 The RBS (B/K) of each habitat type as a function of trawling effort shows that Gravel would be most affected
239 by trawling at all levels of effort (Figure 4), reflecting the higher depletion rates and slower recovery rates
240 (Table 2, Table 3). At swept-area ratios >4.6, the fauna of Gravel were estimated to be fully depleted, with
241 RBS=0 in 18 cells (~2.1%). Most Gravel was not exposed to trawling and ~93.4% of Gravel had RBS >50%. The
242 distribution of RBS values by habitat area (Figure 5) can be used to define other status thresholds; e.g. ~86% of
243 Gravel had RBS >80%. The Gulf-wide average RBS over all Gravel was 91%. Muddy-Sand was relatively more
244 exposed to effort but was less sensitive; the minimum RBS of muddy-Sand was 57% and ~93% had status >80%

(Figure 5). The Gulf-wide RBS of muddy-Sand was 95%. Sand had most exposure to high effort but was the least sensitive habitat (Table 2, Table 3); its Gulf-wide RBS was >98% and >99% of Sand had status >80%. Mud had limited exposure to effort and no exposure to high effort (Table 4); its Gulf-wide RBS was >99% and all Mud cells had status >80%. The spatial distribution of habitat RBS (Figure 6) effectively matches that of trawl effort but with differences in trawled areas due to differences in sensitivity among sediment types. For example, the lowest RBS values were for Gravel in moderate-high effort areas, while neighbouring Sand habitat exposed to similar or greater effort levels had higher RBS values.

The regional average RBS values of the three benthos taxa were similar to those for habitats, in the range ~91–96%. Malacostraca were most affected and Bivalvia least. The absolute status results for taxa differed from their RBS, because they accounted for their distributions. Nevertheless, the Gulf-wide absolute status estimates were similar to average RBS because the abundance of each taxon was about average in trawled areas (Appendix S1).

Discussion

The development of the RBS method is timely because it addresses needs arising from national legislation that incorporates the ecosystem approach to fisheries (FAO 2003) driven by international policy commitments (Rice 2014) and requirements from certification organisations (e.g. MSC 2014) to take account of the impacts of towed bottom-fishing gears on seabed habitats in management plans and fishery assessments. RBS provides a simple quantitative tool for assessing benthic impacts of bottom trawls and other towed fishing gears. The method is widely applicable, including to fisheries where trawl impacts have not yet been assessed, because it requires relatively few data inputs: 1) effort maps that can be derived from commonly collected VMS or tow data; 2) habitat maps that may be available from local regional surveys, or alternatively national or global geoscience databases of sediments provide first-order mapping of habitats (e.g. dbSeabed); 3) impact and recovery parameters, ideally from local experiments linked to habitat classifications used for the seabed where available, but with meta-analyses (as used herein) providing a more widely applicable alternative. Uncertainties in habitat classifications and depletion/recovery rate estimates could be quantified and their implications assessed in future work.

RBS is a level-3 ERAEF method (*sensu* Hobday et al. 2011) that provides continuous quantitative estimates of status with high-resolution at large spatial scales. Geographically, RBS can be applied most broadly for habitats classified by sediment type, because sediment maps are more widely available than maps of other habitat characteristics. RBS can enable assessments of risk framed as: will (or has) the current level of fishing lead to habitat status that compromises a defined sustainability criteria (such as our example: proportion of habitat with $RBS > 50\%$) or management objective (if set, such as our example: regional $RBS > 80\%$)? This flexibility of application cannot be achieved with qualitative or categorical trait-based scoring type assessments and/or non-spatial approaches, which only provide ranking of sensitivity or potential risk (e.g. low, medium, high). Furthermore, there are intuitive relationships between the d and r parameters and traits used for resistance or susceptibility (as measures related to d) and resilience or productivity (measures related to r). Thus, qualitative trait scores might be used to infer likely ranges of d and r , enabling use of quantitative RBS.

Application of RBS to faunal and habitat-forming communities requires local mapping to describe their distributions and, ideally also local information on impact and recovery. Here (Appendix S1), faunal distributions were predicted, using simple linear models, from local data (Kangas et al. 2007) and a few readily available physical variables. In practice, more sophisticated modelling methods could be applied and faunal distributions could be predicted and assessed at species level if required to account for their differing distributions (e.g. Pitcher 2014; Pitcher et al. 2015b). Faunal distribution data from recent surveys may be influenced by past trawling, hence status assessments based on such data allow assessment of current and future impacts but not necessarily past impact. Predicting status due to past impact may be possible (Appendix S1) where trawl effects can be quantified independently of environmental gradients that influence distributions, enabling prediction of un-trawled states (e.g. Ellis et al. 2008; Lambert et al. 2011; Pitcher et al. 2015b).

For our application, we extracted d and r parameters from a published meta-analysis (Collie et al. 2000), which included experimental studies up to the late 1990s. Another meta-analysis included a larger sample size of studies up to the mid-2000s (Kaiser et al. 2006). Future meta-analyses could directly estimate d and r parameters and their uncertainty, as well as quantify links between recovery and environmental variables

other than sediment type, such as temperature and/or primary production — which may enable recovery parameters to account for regional variations in environment. One potential bias when applying RBS to mobile fauna is the possibility that experimentally measured recovery rates reflect movement of individuals into the impacted area, as well as population growth. This bias was accounted for, to an extent, by the adjustment of experimental r to grid-scale R . In future, meta-analysis of faunal abundance across quantified gradients in trawling intensity may be used to estimate grid- R directly.

In our assessment of Exmouth Gulf, habitat RBS and faunal absolute status were affected little at the regional scale, with status $\geq 90\%$ for all habitats and faunal taxa assessed. This was because $< 2\text{--}7\%$ of the region was trawled sufficiently intensely to yield RBS values $< 50\%$ and most of the area was either not trawled or trawled lightly. Further, most high-intensity trawling occurred on Sand, which was relatively resilient. Nevertheless, in regions where trawl effort is more intensive and more widely distributed, larger impacts may be expected. For example, Hiddink et al. (2006b) estimated that bottom trawling in the North Sea had reduced benthic biomass by 56% compared with an un-trawled state, albeit using a different method (size-based benthic community model).

Our application focused on sedimentary habitats but many of the issues surrounding the sustainability and management of bottom trawling relate to status and conservation of biogenic habitats (Rice, Lee & Tandstad, 2015). These habitats are more sensitive to trawling due to higher depletion rates and slower recovery than sedimentary habitats or smaller discrete invertebrates. However, information on distributions of biogenic habitats or habitat-forming benthos is often lacking or inadequate, and parameters for their depletion and recovery rates are also scarce. Some examples where it has been possible to address these information needs include a fish-trawl fishery in the SE of Australia where predicted 2015 regional status of habitat-forming benthos ranged from $\sim 82\%$ to 94% of un-trawled (Pitcher et al. 2015a), and a shrimp-trawl fishery in NE Australia where predicted 2015 regional status ranged from $\sim 76\%$ – 98% (Pitcher et al. 2015b). In both cases, status was predicted to be recovering in 2015 following a series of effort reductions and area closures.

RBS can be used to assess the cumulative effects of multiple bottom-contact fisheries (and potentially other human and environmental pressures causing seabed impacts, if these can be described by parameters

323 analogous to F and d). Further, RBS also supports quantitative evaluation of the effects of alternative fisheries
324 management options (e.g. effort reductions, closed areas and gear modifications) by simulating their
325 implementation and quantifying changes in estimated status. Such evaluations would assist decision-making
326 regarding the choice of management measures to meet environmental targets (e.g. Dichmont et al. 2013) and
327 facilitate progress towards sustainable bottom-contact fishing.

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References

- Astles, K.L., Holloway, M.G., Steffe, A., Green, M., Ganassin, C. & Gibbs, P.J. (2006) An ecological method for qualitative risk assessment and its use in the management of fisheries in New South Wales, Australia. *Fisheries Research*, 82, 290–303.
- Caputi, N., Kangas, M., Denham, A., Feng, M., Pearce, A., Hetzel, Y. & Chandrapavan, A. (2016) Management adaptation of invertebrate fisheries to an extreme marine heat wave event at a global warming hot spot. *Ecology and Evolution*, doi:10.1002/ece3.2137.
- Collie, J.S., Hall, S.J., Kaiser, M.J. & Poiner, I.R. (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology*, 69, 785–798.
- Deng, R., Dichmont, C., Milton, D., Haywood, M., Vance, D., Hall, N. & Die, D. (2005) Can vessel monitoring system data also be used to study trawling intensity and population depletion? The example of Australia's northern prawn fishery. *Canadian Journal of Fisheries & Aquatic Science*, 62, 611–622.
- Dichmont, C.M., Ellis, N., Bustamante, R.H., Deng, R., Tickell, S., Pascual, R., Lozano-Montes, H. & Griffiths, S. (2013) Evaluating marine spatial closures with conflicting fisheries and conservation objectives. *Journal of Applied Ecology*, 50, 1060–1070.
- Ellis, N., Pantus, F.J. & Pitcher, C.R. (2014) Scaling up experimental trawl impact results to fishery management scales—a modeling approach for a 'hot time'. *Canadian Journal of Fisheries & Aquatic Science*, 71, 1–14.
- Ellis, N., Pantus, F.J., Welna, A. & Butler, A. (2008) Evaluating ecosystem-based management options: effects of trawling in Torres Strait, Australia. *Continental Shelf Research*, 28, 2324–2338.
- Eno, N.C., Frid, C.L.J., Hall, K., Ramsay, K., Sharp, R.A.M., Brazier, D.P., Hearn, S., Dernie, K.M., Robinson, K.A., Paramor, O.A.L. & Robinson, L. A. (2013) Assessing the sensitivity of habitats to fishing: from seabed maps to sensitivity maps. *Journal of Fish Biology*, 83, 826–846.

- 357 FAO (2003) Fisheries management. 2. *The Ecosystem Approach to Fisheries*. Food and Agricultural
358 Organisation, Rome.
- 359 Fletcher, W.J., Chesson, J., Fisher, M., Sainsbury, K.J., Hundloe, T., Smith A.D.M. & Whitworth, B. (2002)
360 *National ESD Reporting Framework for Australian Fisheries: The 'How To' Guide for Wild Capture*
361 *Fisheries*. FRDC Project 2000/145, Canberra, Australia. [http://www.fisheries-](http://www.fisheries-esd.com/a/pdf/WildCaptureFisheries_V1_01.pdf)
362 [esd.com/a/pdf/WildCaptureFisheries_V1_01.pdf](http://www.fisheries-esd.com/a/pdf/WildCaptureFisheries_V1_01.pdf)
- 363 Folk, R.L. (1954) The distinction between grain size and mineral composition in sedimentary rock
364 nomenclature. *Journal of Geology*, 62, 344-359.
- 365 Hiddink, J.G., Hutton, T., Jennings, S. & Kaiser, M.J. (2006a) Predicting the effects of area closures and fishing
366 effort restrictions on the production, biomass and species richness of North Sea benthic invertebrate
367 communities. *ICES Journal of Marine Science*, 63, 822–830.
- 368 Hiddink, J.G., Jennings S., Kaiser M.J., Queirós A.M., Duplisea D.E. & Piet G.J. (2006b) Cumulative impacts of
369 seabed trawl disturbance on benthic biomass, production and species richness in different habitats.
370 *Canadian Journal of Fisheries and Aquatic Science*, 63, 721-736.
- 371 Hobday, A.J., Smith, A.D.M., Stobutzki, I., Bulman, C., Daley, R., Dambacher, J., Deng, R., Dowdney, J., Fuller,
372 M., Furlani, D., Griffiths, S.P., Johnson, D., Kenyon, R., Knuckey, I.A., Ling, S.D., Pitcher, C.R., Sainsbury,
373 K.J., Sporcic, M., Smith, T., Walker, T., Wayte, S., Webb, H., Williams, A., Wise, B.S. & Zhou, S. (2011)
374 Ecological Risk Assessment for the Effects of Fishing. *Fisheries Research*, 108, 372–384.
- 375 Jenkins, C.J. (1997) Building Offshore Soils Databases. *Sea Technology*, 38, 25-28.
- 376 Jennings, S. & Kaiser, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology*, 34,
377 201–352.
- 378 Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., Somerfield, P.J. & Karakassis, I. (2006) Global analysis of
379 response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*, 311, 1–14.

- 380 Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S. & Poiner, I.R. (2002) Modification of marine habitats by trawling
381 activities: prognosis and solutions. *Fish & Fisheries*, 3, 114–136.
- 382 Kangas, M.I., Morrison, S., Unsworth, P., Lai, E., Wright, I. & Thomson, A. (2007) *Development of biodiversity*
383 *and habitat monitoring systems for key trawl fisheries in Western Australia*. Final report to Fisheries
384 Research and Development Corporation on Project No. 2002/038. Fisheries Research Report No. 160,
385 Department of Fisheries, Western Australia, 334p
- 386 Lambert, G.I., Jennings, S., Kaiser, M.J., Hinz, H. & Hiddink, J.G. (2011) Quantification and prediction of the
387 impact of fishing on epifaunal communities. *Marine Ecology Progress Series*, 430, 71-86.
- 388 Loneragan, N.R., Kangas, M., Haywood, M.D.E., Kenyon, R.A., Caputi, N. & Sporer, E. (2013) Impact of cyclones
389 and aquatic macrophytes on the recruitment and landings of tiger prawns *Penaeus esculentus* in
390 Exmouth Gulf, Western Australia. *Estuarine, Coastal and Shelf Science*, 127, 46-58.
- 391 McConnaughey, R.A., Mier, K.L. & Dew, C.B. (2000) An examination of chronic trawling effects on soft-bottom
392 benthos of the eastern Bering Sea. *ICES Journal of Marine Science*, 57, 1377–1388.
- 393 MSC (2014) *MSC Fisheries Certification Requirements and Guidance Version 2.0* Marine Stewardship Council,
394 London
- 395 Piet, G.J., Rijnsdorp, A.D., Bergman, M.J.N., Van Santbrink, J.W., Craeymeersch, J. & Buijs, J. (2000) A
396 quantitative evaluation of the impact of beam trawling on benthic fauna in the southern North Sea.
397 *ICES Journal of Marine Science*, 57, 1332-1339.
- 398 Pikitch, E.E.K., Santora, C.C., Babcock, E.E.A., Bakun, A.A., Bonfil, R.R., Conover, D.O., Dayton, P., Doukakis, P.,
399 Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J.
400 & Sainsbury, K.J. (2004) Ecosystem-based fishery management. *Science*, 305, 346–47
- 401 Pitcher C.R., Poiner I.R., Hill B.J. & Burrige C.Y. (2000) The implications of the effects of trawling on sessile
402 megazoo-benthos on a tropical shelf in northeastern Australia. *ICES Journal of Marine Science*, 57,
403 1359-1368

- 404 Pitcher, C.R. (2014) Quantitative Indicators of Environmental Sustainability Risk for a Tropical Shelf Trawl
405 Fishery. *Fisheries Research*, 151, 136–174 <http://dx.doi.org/10.1016/j.fishres.2013.10.024>
- 406 Pitcher, C.R., Burrige, C.Y., Wassenberg, T.J., Hill, B.J. & Poiner I.R. (2009) A large scale BACI experiment to
407 test the effects of prawn trawling on seabed biota in a closed area of the Great Barrier Reef Marine
408 Park, Australia. *Fisheries Research*, 99, 168–183.
- 409 Pitcher, C.R., Ellis, N., Althaus, F., Williams, A. & McLeod, I. (2015a) Predicting benthic impacts & recovery to
410 support biodiversity management in the South-east Marine Region. *Marine Biodiversity Hub, National
411 Environmental Research Program, Final report 2011–2015 Report to Department of the Environment.
412 Canberra, Australia*. (eds N.J. Bax & P. Hedge), pp. 24–25
413 [http://nerpmarinebiodiversity2015.report/predicting-benthic-impacts-and-recovery-to-support-
414 biodiversity-management-in-the-south-east-marine-region/](http://nerpmarinebiodiversity2015.report/predicting-benthic-impacts-and-recovery-to-support-biodiversity-management-in-the-south-east-marine-region/)
- 415 Pitcher, C.R., Ellis, N., Venables, W., Wassenberg, T.J., Burrige, C.Y., Smith, G.P., Browne, M., Pantus, F.J.,
416 Poiner I.R., Doherty P.J., Hooper, J.N.A. & Gribble N. (2015b) Effects of trawling on sessile
417 megabenthos in the Great Barrier Reef, and evaluation of the efficacy of management strategies. *ICES
418 Journal of Marine Science*, 73, i115–i126. http://icesjms.oxfordjournals.org/content/73/suppl_1/i115
- 419 Rice, J., Lee, J. & Tandstad, M. (2015) Parallel initiatives: CBD's Ecologically or Biologically Significant Areas
420 (EBSAs) and FAO's Vulnerable Marine Ecosystems (VMEs) criteria and processes. *Governance of
421 Marine Fisheries and Biodiversity Conservation: Interaction and Coevolution* (eds S.M. Garcia, J. Rice &
422 A. Charles), pp. 195–208, John Wiley and Sons, New York.
- 423 Rice, J.C. 2014. Evolution of international commitments for fisheries sustainability. *ICES Journal of Marine
424 Science*, 71, 157–165.
- 425 Rijnsdorp, A.D., Buys, A.M., Storbeck, F. & Visser, E.G. (1998) Micro-scale distribution of beam trawl effort in
426 the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed
427 and the impact on benthic organisms. *ICES Journal of Marine Science* 55, 403–419.

- 428 Schaefer, M.B. (1954) Some aspects of the dynamics of populations important to the management of
429 commercial marine fisheries. *Bulletin of the Inter-American Tropical Tuna Commission* 1, 27–56.
- 430 Sinclair, M. & Valdimarsson, G. (2003) *Responsible fisheries in the marine ecosystem*, Food and Agricultural
431 Organisation, Rome.
- 432 Smith, A.D.M., Fulton, E.A., Hobday, A.J., Smith, D.C. & Shoulder, P. (2007) Scientific tools to support practical
433 implementation of ecosystem based fisheries management. *ICES Journal of Marine Science*, 64, 633–
434 639.
- 435 Stobutzki, I.C., Miller, M.J. & Brewer, D.T. (2001) Sustainability of fishery bycatch: a process for assessing highly
436 diverse and numerous bycatch. *Environmental Conservation*, 28, 167–181.
- 437 Williams, A., Dowdney, J., Smith, A.D.M., Hobday, A.J. & Fuller, M. (2011) Evaluating impacts of fishing on
438 benthic habitats: a risk assessment framework applied to Australian fisheries. *Fisheries Research*, 112,
439 154-167.
- 440 Zhou, S. & Griffiths, S.P. (2008) Sustainability Assessment for Fishing Effects (SAFE): A new quantitative
441 ecological risk assessment method and its application to elasmobranch bycatch in an Australian trawl
442 fishery. *Fisheries Research*, 91, 56–68.
- 443

Tables

Table 1. Impact (*i*) as log(response ratio) from figure 2 in Collie et al. (2000). All terms include the overall mean log response (−0.79). (a) Gear-by-habitat effects were inferred assuming main effects were additive and ignoring interactions (shaded); (b) taxa-by-habitat effects for otter trawl (for three of 12 taxa).

		Habitat main effect			
(a)		Mud	muddy-Sand	Sand	Gravel
Gear main effect	<i>i</i>	−0.63	−0.84	−0.79	−0.98
intertidal dredging	−1.91	−1.75	−1.96	−1.91	−2.10
scallop dredging	−1.09	−0.93	−1.14	−1.09	−1.28
intertidal raking	−1.07	−0.91	−1.12	−1.07	−1.26
beam trawling	−0.56	−0.40	−0.61	−0.56	−0.75
otter trawling	−0.47	−0.31	−0.52	−0.47	−0.66
		Inferred effects for otter trawling			
(b)		Mud	muddy-Sand	Sand	Gravel
Taxa main effect	<i>i</i>				
Polychaeta	−0.80	−0.32	−0.53	−0.48	−0.67
Malacostraca	−1.36	−0.88	−1.09	−1.04	−1.23
Bivalvia	−0.50	−0.02	−0.23	−0.18	−0.37

Table 2. Depletion rates (d) for habitats and taxa, by otter trawl. Taxa-by-habitat estimates were inferred assuming main effects were additive and ignoring interactions (shaded). The taxon rates for *All habitats* were derived by first adjusting the taxa main effects in Table 1 for the otter trawl effect and subtracting the overall mean response (i.e. adding $-0.47 - (-0.79) = 0.32$) then applying eqn 4.

	All habitats	Mud	muddy-Sand	Sand	Gravel
Taxon ↓, All taxa→	d	0.27	0.41	0.37	0.48
Polychaeta	0.38	0.27	0.41	0.38	0.49
Malacostraca	0.65	0.59	0.66	0.65	0.71
Bivalvia	0.16	0.02	0.21	0.16	0.31

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Table 3. (a) Logistic recovery rates (r , year⁻¹), for habitats and taxa, estimated by non-linear regression fitted to recovery curves in figure 5 of Collie et al. (2000); taxa-by-habitat recovery estimates were inferred assuming main effects were additive and ignoring interactions (shaded). (b) Grid-scale R estimated by adjusting r , using eqn 3.

	All habitats	Mud	muddy-Sand	Sand	Gravel
(a) Taxon ↓, All taxa→	r	6.4	5.3	15.6	3.0
Polychaeta	5.8	4.9	4.0	11.9	2.3
Malacostraca	6.0	5.0	4.1	12.2	2.4
Bivalvia	3.6	3.0	2.5	7.4	1.4
(b) Taxon ↓, All taxa→	R	5.5	4.1	12.5	2.2
Polychaeta	4.6	4.2	3.1	9.5	1.7
Malacostraca	3.7	3.3	2.5	7.6	1.4
Bivalvia	3.3	3.0	2.2	6.8	1.2

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Table 4. Habitat areas and trawled areas (km²) by base 2 categories of trawl swept-area ratio (area trawled/grid-cell area): total area; area of sediment habitat types; total swept area; and estimates of trawl footprints (which account for overlapping trawls) assuming trawling is uniform at 0.01° or randomly distributed within 0.01° grid cells.

Swept-area ratio	Total area	Habitat area				Swept area	Trawl footprint	
		Mud	muddy-Sand	Sand	Gravel		Uniform	Random
0	1760	34	244	892	590	0	0	0
>0–0.03125	454	9	94	234	117	9	9	8
0.0625	126	1	32	66	26	11	11	11
0.125	152	2	57	66	26	28	28	25
0.25	210	0	79	95	36	74	74	62
0.5	222	2	42	136	41	160	160	113
1	307	6	100	151	50	451	307	233
2	216	0	42	121	53	590	216	200
>4	88	0	8	53	28	481	88	88
Totals	3,535	55	698	1,815	967	1,803	892	740

471

472 **Figure captions**

473

474 **Figure 1.** Schematic representation of a trawl impact and recovery experiment, with changes in abundance (B)
475 as a proportion of carrying capacity (K) described with the logistic equation. Abundance is depleted from K to
476 B_0 by experimental trawling at time 0 depending on depletion rate d and number of trawls T , i.e. $B_0=(1-d)^T$.
477 Recovery follows at rate r so that abundance is B_t after time t , eventually approaching K asymptotically.

478

479 **Figure 2.** Map of sedimentary habitats in Exmouth Gulf, between 1–50 m depth (contours: 10 m intervals).
480 Inset: ternary (triangle) plot showing classification of mud, sand and gravel grain-size fractions (0–1) to
481 habitats.

482

483 **Figure 3.** Map of trawl effort in Exmouth Gulf, as annual swept-area ratio per grid-cell, between 1–50 m depth
484 (contours: 10 m intervals).

485

486 **Figure 4.** Proportion of total Exmouth Gulf area and cumulative total area by annual trawl swept-area ratio
487 (base 2); with cumulative distributions of area for each sediment-habitat type; and equilibrium status (B/K) of
488 habitats at each level of (constant) trawl intensity.

489

490 **Figure 5.** Relative benthic status (RBS) of Exmouth Gulf total area and each sedimentary habitat against
491 cumulative proportion of habitat area, ordered by trawl effort, indicating the proportion of area above or
492 below any given status.

493

494 **Figure 6.** Map of relative benthic status (RBS) of seabed in Exmouth Gulf, accounting for differing sensitivity of
495 sedimentary habitat types.

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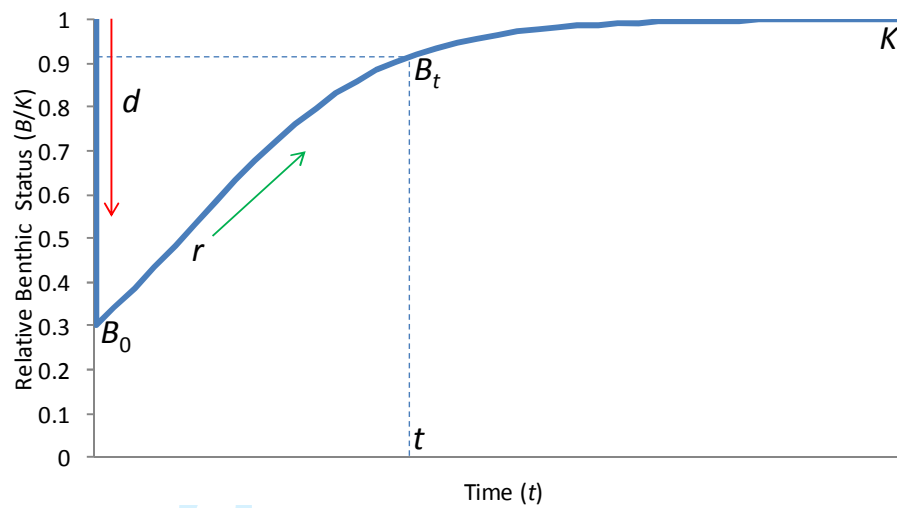
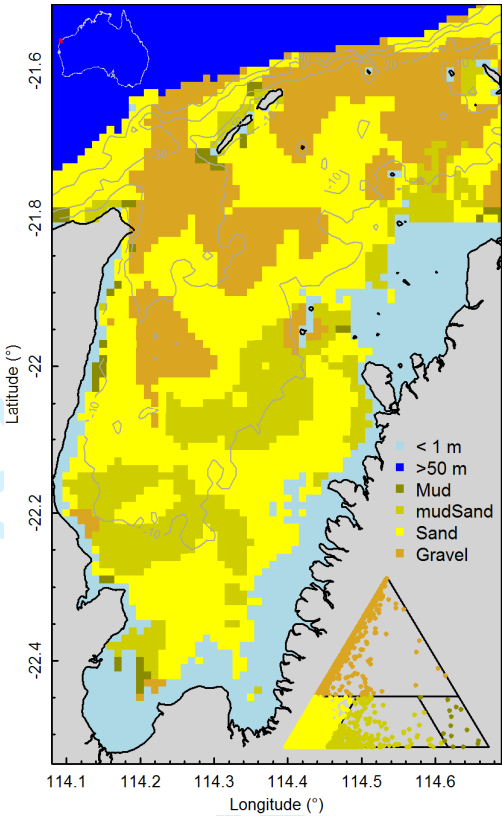


Figure 1. Schematic representation of a trawl impact and recovery experiment, with changes in abundance (B) as a proportion of carrying capacity (K) described with the logistic equation. Abundance is depleted from K to B_0 by experimental trawling at time 0 depending on depletion rate d and number of trawls T , i.e. $B_0 = (1-d)^T$. Recovery follows at rate r so that abundance is B_t after time t , eventually approaching K asymptotically.

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Figure 2. Map of sedimentary habitats in Exmouth Gulf, between 1–50 m depth (contours: 10 m intervals). Inset: ternary (triangle) plot showing classification of mud, sand and gravel grain-size fractions (0–1) to habitats.

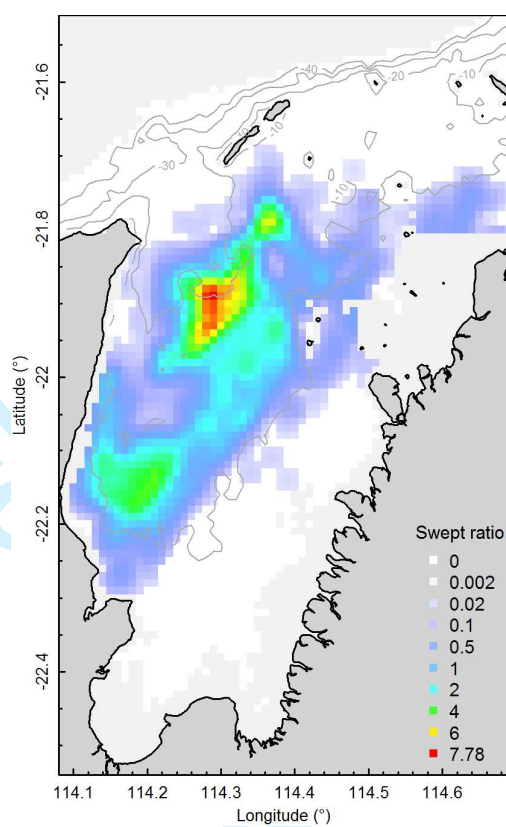
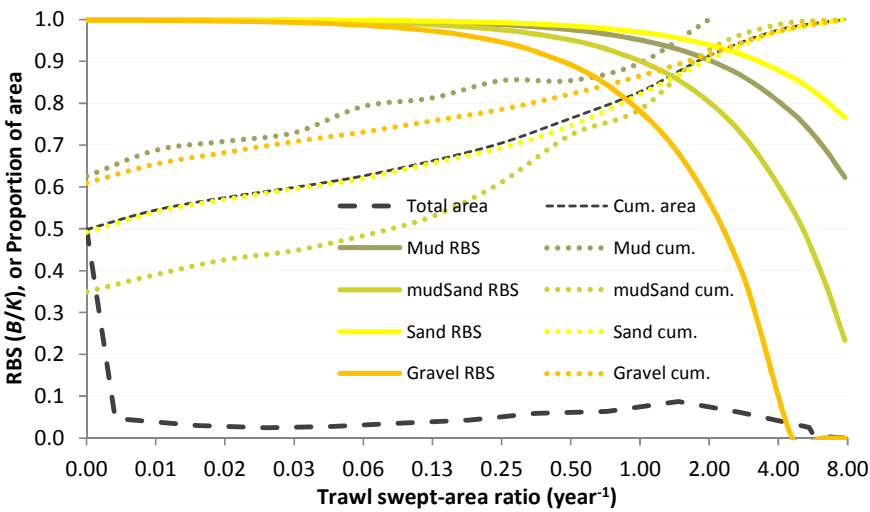


Figure 3. Map of trawl effort in Exmouth Gulf, as annual swept-area ratio per grid-cell, between 1–50 m depth (contours: 10 m intervals).

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Figure 4. Proportion of total Exmouth Gulf area and cumulative total area by annual trawl swept-area ratio (base 2); with cumulative distributions of area for each sediment-habitat type; and equilibrium status (B/K) of habitats at each level of (constant) trawl intensity.

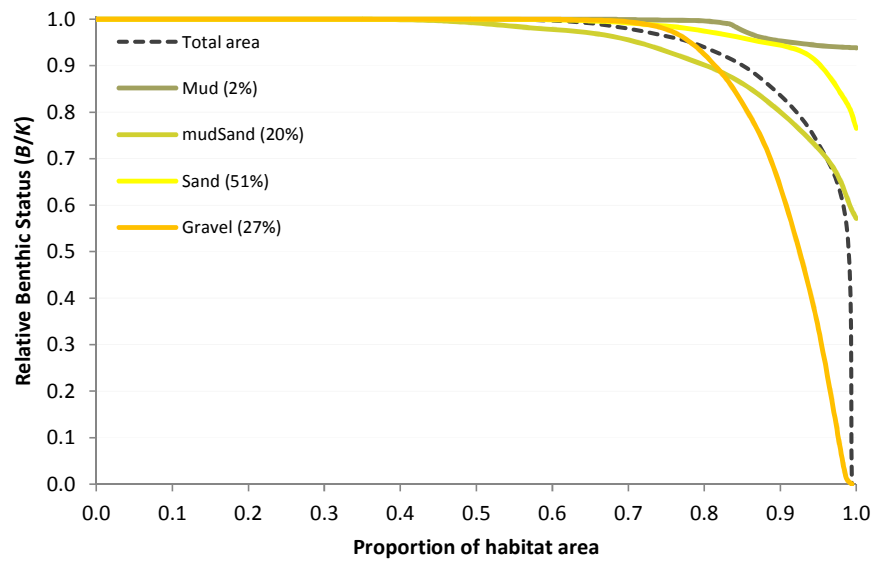
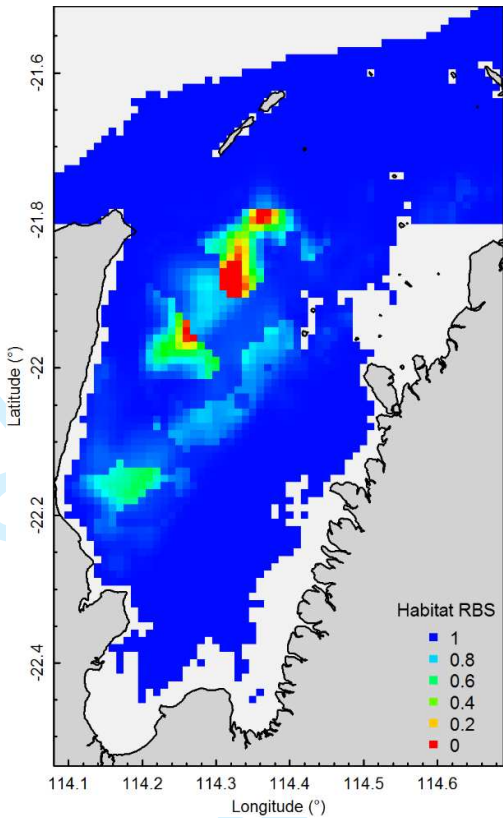


Figure 5. Relative benthic status (RBS) of Exmouth Gulf total area and each sedimentary habitat against cumulative proportion of habitat area, ordered by trawl effort, indicating the proportion of area above or below any given status.

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Figure 6. Map of relative benthic status (RBS) of seabed in Exmouth Gulf, accounting for differing sensitivity of sedimentary habitat types.

540

541 **Supporting Information**

542 Additional Supporting Information may be found in the online version of this article:

543 **Appendix S1.** *Methods and results for benthic faunal status assessment.*

544

545 **Author Contributions Statement**

546 CRP and NE conceived and developed the model, MK provided fishery data, CRP implemented the model and
547 led writing of the manuscript. All authors contributed to review and integrity of the work, interpretation of
548 results, drafting and revising the manuscript content and final approval for publication.